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Determinants of community structure in plants and animals

ABSTRACTS

R. Arditi (Institut de zoologie et d'écologie animale, Université-Dorigny, 1015 Lausanne et Écologie des populations et communautés, Bâtiment 362, Université Paris-Sud XI, F-91405 Orsay Cedex, France): Stability and complexity – what do density – dependent food webs bring?

The link between complexity and stability is one of the oldest theoretical questions of community ecology. Based on the observation that complex ecosystems (e.g., tropical forests) incurred apparently small fluctuations, the accepted viewpoint for 50 years was that complexity generated stability. In the early 70's, May's theoretical work reversed the paradigm: mathematical models of randomly assembled communities showed that the more complex they were, the less probable that they would be stable. This work was later refined and more thoroughly developed by Pimm in the context of food webs. An important restriction of May's models was that they were linear, assuming that communities were always close to equilibrium. Although Pimm investigated non-equilibrium situations, he assumed that trophic interactions were density-independent, i.e., that the amount of resources consumed by an individual consumers did not depend on the number of conspecifics. Presently, there is little doubt that density-dependence is frequent in nature as well as in laboratory conditions. Model food webs with strong density-dependence are not easy to develop. One type of such model will be presented. First results show that these webs possess unique properties that could not be foreseen from density-independent models. These properties make them more realistic and suggest a possible reconciliation between theoretical predictions and empirical observations.

C. Arnold, A. Buttler & B. Werffeli (University of Neuchâtel, Switzerland): Ecological determinism of bryophyte community patterns in alluvial steppes.

Alluvial steppes are brushwood communities characterised by xero-thermophilous species. Despite these steppes represent functional units with increasing disconnection to the alluvial system, they reveal the highest species pool (184 herbaceous species) among all the communities recorded in the Swiss alluvial zones of national importance, after the White Alder flood plain forest (about 250 species). Unfortunately, as a transitional stage, where the bank cannot be reached any longer by the river, *Picea abies* becomes an invasive species and *Pinus silvestris* and *Betula pendula* may grow tall, turning the general ecological conditions towards a more forested environment, with a related loss of species diversity.

In this paper we aim at understanding, by means of spatial multivariate statistics, the ecological determinism of the Bryophyte community patterns. Three plots representing a successional gradient towards a tree dominated environment are investigated. It is shown how the vegetation structure changes in relation to the shift from exogenous to endogenous ecological conditions and how the spatial component can be used in detecting some structural features.

T.C.M. Bakker, D. Mazzi & S. Zala (Zoologisches Institut, Universität Bern): Enhanced transmission of the parasite *Pomphorhynchus laevis* through behavioural and colour changes in its intermediate host, *Gammarus pulex*.

Parasites with a complex life cycle involving several host species often induce changes in their intermediate hosts. The parasite-induced changes make the intermediate host a more profitable prey to the next host of the parasite thereby increasing the chances of transmission of the parasite.

The acanthocephalan parasite *Pomphorhynchus laevis* is transmitted by the amphipod *Gammarus pulex* to its next host, fish. The parasite is clearly visible through the transparent cuticle of *G. pulex* as a conspicuous orange spot. Additionally, with the onset of infectivity of *P. laevis* to its next host, *G. pulex* shows a changed photoreaction; it becomes photophilic and positively phototactic. Hungry stickleback fish, *Gasterosteus aculeatus*, preferred to eat infected *G. pulex* over uninfected ones. By means of experimental manipulation of the colour effects of the parasite in its intermediate host, we showed for the first time that both behavioural and colour changes in the intermediate host promote parasite transmission in such acanthocephalan systems.

A. Baur, L. Fröberg & B. Baur (Institut für Natur-, Landschafts- und Umweltschutz, Universität Basel; Dept. of Systematic Botany, University of Lund): Herbivory in a calcicolous lichen community: effects of selective snail grazing.

The land snails *Chondrina clienta* and *Balea perversa* coexist on old stone walls where they feed on calcicolous lichens. Previous studies showed that both intra- and interspecific competition most probably for food occur in these species. A total of 32 calcicolous lichen species, one alga and one bryophyte were recorded on a limestone wall in the grassland Great Alvar on the Baltic island of Oland, Sweden. Fourteen (41%) of these 34 species and free-living cyanobacteria showed herbivore damage, most probably due to grazing by the land snails *Chondrina clienta* and *Balea perversa* that inhabited the limestone wall. Three laboratory experiments were conducted to examine the food preferences of individuals of *C. clienta* and *B. perversa* collected at this site and to evaluate any association between their preference and the net food quality of the lichens to the snails. *C. clienta* and *B. perversa* exhibited food preferences, which differed significantly between species. Within species, variation in food choice was similar among individuals. This indicates that snail populations may be composed of polyphagous individuals with similar food preferences. Different lichen species were of different net food quality to the snails as indicated by growth rate differences. In both snail species the most preferred lichen species of the choice experiment caused the largest weight increase in juveniles, viz. *Caloplaca flavovirescens* in *C. clienta* and *Aspicilia calcarea* in *B. perversa*. This suggests that the snail species studied differ in their abilities to deal with secondary compounds and physical characteristics of certain lichens or that they can utilize the energy and nutrients of these lichens to a different extent. It is suggested that differential food preferences might reduce the intensity of interspecific competition for resources (lichens) between *C. clienta* and *B. perversa*.

G. Bernasconi & L. Keller (Universität Bern, Ethologische Station; IZEA, Université de Lausanne): Reproductive conflicts in cooperative associations of Fire Ant queens (*Solenopsis invicta*).

In ants unrelated queens frequently associate to initiate a colony cooperatively. The joint reproductive effort of the cofoundresses increases growth and survival of the incipient colony. Yet, such associations are unstable. Soon after emergence of the first workers, queen-queen and queen-worker fights lead to the death or expulsion of all but one cofoundress. Because no sexual offspring are produced in incipient colonies the surviving queen mono-

polises the entire future reproductive success of the colony. Two factors, the queens' relative fighting ability and their relative contribution to worker production (assuming that workers can recognize and selectively favour their mother) have been proposed to influence the survival prospects of individual queens within associations. The effect of these two factors were tested in the fire ant *Solenopsis invicta*. Initial size differences, a potential measure of the queens' fighting ability, affected the outcome of the conflicts, so that the initially heavier queen was more likely to survive. Differential weight loss by initially equal nest mates was also related to survival, with the queen losing more weight being more likely to die. The manipulation of the queens' relative contribution to the worker brood had no significant effect on the queens' survival probability, suggesting that workers are unable to favour their mother.

L. Bersier & G. Sugihara (Scripps Institution of Oceanography, UC San Diego): Scale invariance versus scale dependence in food web properties.

There is a current controversy as to the scaling behaviour of food web properties. Earlier studies based on large collections of food webs found that some food web properties (e.g., the link density, the fractions of top, intermediate and basal species) were scale invariant: they remained constant across webs of different sizes. These scaling properties fostered the formulation of interesting hypotheses on how food webs are assembled and how they operate. However, together with criticisms of the data used to demonstrate these properties, recently compiled food webs have cast doubt on the validity of the scale invariant laws. Moreover, the scale invariance found in some data sets has recently been challenged. The properties may indeed vary with web size. The scale dependent hypothesis appears to be the new paradigm in food web theory. Here, we review the evidence in favour of both hypotheses, and show that the scale dependent hypothesis is weakly supported empirically. More specifically, for one large collection of food webs, we analyze systematically a suite of competing models describing the relationship between food web properties and web size. We present quantitative evidence that the most robust model is a piecewise linear regression, indicating that food web properties are bounded to different scaling regions. The properties of small webs exhibit scale dependence, while they are scale invariant for large webs. Finally, we discuss the generality of the link density property, and point out its extreme sensitivity to sampling effort.

W. Brown (Institut de Zoologie et d'Écologie Animale, Université de Lausanne): Female choice for an indicator of male competitiveness in the Black-horned Tree Cricket.

Although evidence of mate choice is now well founded, distinguishing among alternative evolutionary models of female choice remains problematic. An approach that has been surprisingly under-utilized is the study of functional design or teleonomy. Models of sexual selection make fundamentally different predictions about the way in which preferences should be structured. I studied the design of female choice for song in Black-horned Tree Crickets, predicting from indicator models that choices should be (1) based on comparisons, (2) directed at elements of sex-limited signals that indicate fecundity benefits and/or heritable fitness, and (3) these elements should lack susceptibility to cheating. These predictions were contrasted with the predictions from runaway models that choices should (1) be fixed within females and (2) show consistent variability among females. Results showed that comparisons were necessary for choices, females preferred low-frequency songs, and low frequency was a reliable indicator of both fecundity and putative heritable benefits of mating, supporting all 3 predictions of indicator models. By contrast, female preferences were neither fixed within nor variable among females, falsifying the necessary conditions for runaway selection. Combining these results with genetic studies of mate choice will determine the model of sexual selection that is operating on cricket song.

P. Charlier, P. Furst, G. Blandenier & S. Pozzi (Plant Ecology and Biogeography Laboratory, University of Geneva; Laboratory of Animal Ecology, University of Neuchâtel; Natural History Museum of Geneva): Arachnological and botanical transect from a forest's rim to a wet meadow.

We studied in 1992 and 1993 the characteristics of spiders' communities of small natural areas with ecological conditions as wide as an Oak forest's rim (*Quercus robur*, *Q. petraea*), a wet meadow containing mainly *Molinia arundinacea* and a sword-flag (*Gladiolus paluster*) and a tilling field in full regeneration. All these plant communities are gathered on a 35 meters long line. What are the variations, speaking of specifications and quantities of spiders' communities in the wet meadow:— over a year from March to October 1992; — with three different kinds of mowing management? The trapping's method of Barbers has been used.

I. Dajoz, J. Shykoff, Y. Loublier, M.H. Pham-Delegue & I. Till-Bottraud (Laboratoire d'Écologie, Université de Paris 6; ESV, Université de Paris 11; Institut für experimentelle Ökologie ETH Zürich; Neurobiologie Comparée des Invertébrés, INRA; Biologie des Populations d'Altitude, Université de Grenoble): Pollinator mediated selection on pollen morphology in the genus *Viola*.

Many plants produce several pollen morphs differing in aperture number. Species of *Viola* exhibit this heteromorphism, with pollen with 3–6 apertures. The more apertures a pollen grain has, the more quickly it germinates, but the shorter its life-span is. Theoretical models find an ESS for several pollen morphs. Models predict a higher proportion of many-aperture pollen grains on plants that receive more pollinator visits. Lastly, variation in ploidy level can lead to variation in pollen aperture number. Our aim in this paper is to address the following questions:

What is the distribution of pollen heteromorphism in *Viola*? Is pollen heteromorphism in *Viola* solely due to variations in plant ploidy level? Or, can selection act on proportions of different morphs? What is the nature of this selection?

For the 2 subgenera of *Viola*: pansies (18 spp.) are heteromorphic, with no correlation between chromosome number and mean aperture number. In violets (12 spp.) those with $2n = 20$ are monomorphic, those with $2n = 40$ are heteromorphic.

In pansies there is a negative correlation between elevation of collection site and mean aperture number. This agrees with our predictions of the model: pollination limitation at high elevation should select for low aperture number.

Within species, there is a positive correlation between flower or spur size, and mean aperture number. Also, pollinators prefer large flowers.

These data suggest that some selection pressures act on pollen grain morphology, and that these selective pressures are partly due to differences in pollinator activity.

M. Fischer & D. Matthies (Institut für Umweltwissenschaften, Universität Zürich): Conservation biology of rare grassland plants in the Swiss Jura mountains.

In a comparison of vegetation records from 26 grasslands in the Swiss Jura mountains from 1950 and 1985 short-lived species with low local abundance and high habitat specificity showed the highest rates of local extinction. The biennial *Gentianella germanica* belongs to this group. Populations of *G. germanica* had a low mean annual population growth rate (0.84) with large spatial (among seven sites) and temporal variation (among the years 1993–95). In a survey of 23 populations number of seeds per plant was reduced in small compared with large populations. The population growth rate estimated from the number of flowering plants 1993, 94 and 95 showed the same pattern. This could be due to poorer habitat quality, disruption of plant-pollinator mutualism or genetic erosion in small populations. However, habitat properties did not explain the pattern and hand pollination did not increase seed set as compared with open pollination, whereas genetic variation as measured with RAPD-PCR was reduced in

smaller populations. Management of the species should avoid disturbance during the time of flowering or fruit set and allow disturbance that leads to the creation of vegetation gaps, because it improves seedling establishment. Conservation biology should integrate from the gene to the community, use descriptive and experimental methods and study spatial scales comprising several to many populations.

D. Fraefel, M. Haffner & V. Ziswiler (Zoologisches Museum der Universität Zürich): Morphological and micro-anatomical investigations of the integument of the European red squirrel *Sciurus vulgaris* L., 1758 (Mammalia, Rodentia).

The Red squirrel *Sciurus vulgaris* shows adaptations in its body for the arboreal way of life. Morphological and micro-anatomical investigations of the integument of different parts of the body were carried out to find such adaptations and relate them to their functions. The Red squirrel has vibrissae on the head, on the forelimbs, on the breast and on the abdomen. While the number of Vibrissae mystaciales and the Vibrissae anconaeales is constant, the number of the other vibrissae shows an intraspecific variability. For the first time an accumulation of apocrine glands was found on the chin of the Red squirrel. These glands occur on both sides of the chin near the corner of the mouth and are present in both sexes. The secretions may be spread on the head with the forefeet during face-wiping. Eccrine glands occur in all foot pads. Instead of the tarsal pads, sparsely haired areas occur on the heels. There, the hairs are equipped with enlarged sebaceous glands. The secretions of these glands may be used for scent-marking the frequently visited feeding places. The forefeet are adapted to grasp twigs and handle food. Both carpal pads contain muscles and cartilage. They provide, together with the reduced first digit, an abutment against the grasping digits two to five.

J. Frantzen (Institut de biologie végétale, Université de Fribourg): Avoidance and resistance in the weed pathosystem *Senecio vulgaris* L.–*Puccinia lagenophorae* Cooke.

The rust fungus *P. lagenophorae* might be used to control the annual weed *S. vulgaris*. A system management approach of biological weed control, which is followed to study the suitability of *P. lagenophorae* as biological control agent, is presented. The system management approach both depends on, and also provides, fundamental knowledge of mechanisms at the individual and population level. One study of the ongoing research was directed to the disease defence mechanisms of avoidance and resistance in the weed pathosystem *S. vulgaris*–*P. lagenophorae*.

In an integrated approach, three plant lines of *S. vulgaris* were tested for avoidance of, and resistance to infection by *P. lagenophorae*. Differences in susceptibility to *P. lagenophorae* infection between plant stages were determined independent of plant line. Plant lines differed also in growth rate, and so, the fraction of plants in the most susceptible plant stage at the time of inoculation differed between plant lines. The combination of the effects of plant stage on infection and plant line on growth rate resulted in differences in avoidance of *P. lagenophorae* infection between plant lines. Differences in resistance to *P. lagenophorae* infection between plant lines were determined in one of the two experiments. The results are discussed with respect to the impact of pathogens on plant populations.

J. Georgakopoulos, J. Berlie, V. Derivaz & B. Reverdin (Laboratoire d'Éthologie, Université de Genève, rte des Acacias, 1227 Carouge): Structuring space through path integration.

Recent theories of navigation postulate that path integration may be linked with a stable representation of space. Thus, the subject can constantly update its position on this "map" by keeping track of its own movements through path integration. Likewise, path integration may be used during exploration to place relevant sites or cues in space. The first experiment studies

the interaction between path integration and visual cues in golden hamsters (6 subjects). The subjects are trained to find food in one of four identical cylinders which are distinguishable only by their location. No other visual cues are present. In test trials, the subject is led in darkness along a new path to a given release point. The light is then switched on and the animal goes to the food source on its own. The subjects chose the correct cylinder in 86% of test trials. This successful orientation can be explained in two ways: 1) By keeping track of its movements through familiar space, the subject can anticipate a given visual panorama. When the light comes on, it can then compare what it sees with this anticipated view in order to identify the correct goal. The goal can then be reached using the visual cues. 2) The hamster may orient towards a point in absolute space independently of visual cues, by storing a vector linked to the position of the goal. It can then at any moment locate the goal by combining the short-term vector derived from path integration (which gives the animals present location) with the memorised vector associated with the goal. The second possibility was verified by repeating the first experiment in total darkness. In a high percentage of trials (33%) the subjects refused the task. However, when the animals attempted to reach the goal they succeeded in 99% of these trials (64% of the total). In a final experiment no external cues mark the goal. All hoarding trips are carried out in total darkness, eliminating visual information. The animal is trained to find food in a constant location. In test trials it is led along a new path to a given release point from which it must go to the goal. In this situation, where nothing indicates that the goal has been reached, the animals usually do not stop at the correct location. However, in 56% of trials, the subject reaches this location by a fairly straight path (up to 1.5 times the shortest possible path). These last two experiments suggest that hamsters are indeed able to use path integration in conjunction with their knowledge of a familiar environment; nevertheless, path integration appears to require additional confirmation before the subject acts on this information.

L. Gigord (Laboratoire d'Évolution et Systématique, Université Paris XI-CNRS, Laboratoire de Biologie et Physiologie Végétale, Université de La Réunion; Conservatoire National Botanique de Mascarin, Ile de La Réunion): Inbreeding depression in two natural and fragmented populations of an endemic and self-incompatibility tree of La Réunion Island (Mascarenes Archipelago, Indian Ocean): '*Dombeya acutangula* Cav. (Sterculiaceae).

La Réunion Island resembles other volcanic islands (Hawaii, Galapagos...) with exceptional flora of approximately one thousand of endemic and indigenous species. Habitat fragmentation has reached a critical level within forest formations at low altitude with ever increasing anthropisation following the arrival of man three centuries ago. The lack of biodiversity and rapidly decreasing habitat have become a major concern for the various island authorities.

This study is to examine the consequences of fragmentation of natural habitat on a species endemic of the archipelago: *Dombeya acutangula* Cav. Two very different island populations have been examined: one very fragmented (close to a highly anthropomorphised region and organised in groups of variable sizes (3 to 10 individuals) and another not fragmented in a natural reserve. Cross breeding experiments between individuals from the two populations was carried out to find the level of decrease in consanguinity in descendants according to the geographical distance between the individuals. The following cross-breeds were realised: self-fertilization without human intervention, self-fertilization with human intervention, within-population crosses between neighbouring individuals, within-population crosses between distant individuals and between-population crosses. Addition crosses breeding between individuals from these Réunion populations and other individuals from a neighbouring island (Mauritius) were also carried out. Fitness components of descendants from these cross-breeds were measured (number of seeds per flower, weight of seeds, germination rate, growth, etc...). The most striking result of the study shows that there is no significant difference

between the descendants as a whole, except for those emerging from cross breeding between individuals originating from the same deme in the fragmented population. In these individuals, this cross breeding leads to the production of significantly weaker and smaller seeds than those produced by the non fragmented population.

M. Gosteli (Natural History Museum, Bernastrasse 15, CH-3005 Bern): Ecological relationships between snail communities and vegetation.

An inventory of the snail fauna was taken at 33 sample sites situated in four different habitat types near Merischausen in the northern Swiss Jura. To gain information about microclimate and soil quality in a given habitat plant communities and their ecological indicator values known from literature were scored at the sites. Snail faunas and plant communities are significantly correlated, indicating that ecological requirements of snails and plants occurring at the same site are similar. Both depend on microclimatic conditions as humidity, light, temperature and on soil factors as permeability, pH and nutrient content. However, the relatively low similarity coefficient of 0.5 between communities of snails and plants indicates that there may be other ecological factors (a biotic or biotic) influencing snails and plants in a different manner.

M. Haffner (Zoologisches Museum, Universität Zürich): Adaptations to digging and climbing in the sole of the feet of some small mammals.

The feet of nine species were studied by means of gross morphology and microscopical anatomy. Adaptations to digging and climbing were found in the integument and the claws. The palms of *Talpa europaea* are smooth. They have neither pads nor glands, for any elevation or moist surface would hinder the soil from rolling. Although *Arvicola terrestris* cuts soil with its incisors, the reduced number of foot pads, their flatness and the glandless sole indicate that the feet are used as shovel-like tools. Bats climb by hooking their long, curved claws into crevices and cracks. Foot pads are absent, but regions with a thickened epidermis reflect increased mechanical strain. *Rhinolophus ferrumequinum*, which is specialised in hanging on twigs while hunting insects, has epidermal thickenings at the soles of the middle phalanges of the toes. When *Myotis myotis* walks or climbs on horizontal surfaces the bearing part of the wing is the scutelliform-shaped integumentary thickening on the wrist, while in the hind feet the thickened soles of the first toes are mainly loaded. In *Micromys minutus* nap-shaped integumentary thickenings with eccrine glands at the base of the toes and around the carpal pads are adaptations to climbing by grasping stacks. *Muscardinus avellanarius* can climb by pressing the soles of its feet against the bark which is reflected by big softpads with a huge amount of eccrine glands.

B. Hägele & M. Rowell-Rahier (Zoologisches Institut der Universität Basel: Institut de Zoologie, Université de Neuchâtel): The choice and performance of two generalist and two specialist insect herbivores towards cacalol and seneciphyllin, a sesquiterpene and a pyrrolizidine alkaloid found in *Adenostyles alpina* (Asteraceae, Senecioneae).

Potential deterrent or attractive effects of two chemicals (cacalol, seneciphyllin and the combination of both) were tested in a first set of three experiments in standard leaf disk choice experiments. In a second set of experiments the same compounds were force fed to all species by painting them on leaf disks which were fed to the larvae over a period of ten to 15 days. The effects on the performance of the four species could be assessed by comparing the growth of the groups fed the leaf disks treated with the chemicals to those fed with disks treated with the solvent only. Larvae of the specialist leaf beetles *Oreina cacaliae* and *O. speciosissima* (Coleoptera, Chrysomelidae) showed neither an attractive nor a repellent reaction towards the

two chemicals when tested individually. The combination of both chemicals however was repellent to both species. Larval growth of the two leaf beetle species was not influenced by the experimental treatments. Larvae of the generalist *Cylindrotoma distinctissima* (Diptera, Tipulidae) were repelled by the cacalol, seneciphyllin and the combination treatment. Larval growth was reduced by all treatments except the alkaloid high concentration treatment. Caterpillars of the generalist *Callimorpha dominula* (Lepidoptera, Arctiidae) were repelled by cacalol and the combination treatment and not affected by the seneciphyllin treatment. After experience with seneciphyllin however it became attractive to the caterpillars. The high dose combination treatment was also effective in reducing growth of the caterpillars. Growth in all other treatments was not different from the control group.

L. Heer (Zoologisches Institut, Universität Bern): Intense sperm competition in the polygynandrous Alpine Accentor (*Prunella collaris*).

Alpine Accentors are breeding in groups consisting of 3–5 males and 2–3 females. All males of one unit compete for the access to fertile females within their breeding group. Of 7 females, focus animal samplings were performed to work out the role of females in controlling copulations. Alpine Accentors have a high copulation frequency and males do guard their mates closely to enhance their certainty of paternity. Females show fertility-advertisement by displaying themselves on elevated rocks and uttering long series of calls. Further, females actively seek out males what normally results in intense flight pursuits. The females are mainly responsible for soliciting copulations. Paternity is multiple in Alpine Accentors with up to three males siring young within one clutch. Results of DNA fingerprints indicate that frequent copulations and intense mate guarding do not ensure one male's full paternity in such a promiscuous system.

B. Hellriegel (Zoologisches Museum, Universität Zürich-Irchel, Winterthurerstr. 190, 8057 Zürich): Sperm competition in Diptera: adding the female perspective.

Sperm competition has traditionally been modelled exclusively from the male perspective; females have been taken as passive during the entire process. However, many female insects have a complex reproductive system which suggests a function in postcopulatory female choice to control or at least influence the paternity of their offspring. One of the traits constituting this complexity is the presence of multiple sperm stores; many female flies have two or three spermathecae.

The main purpose of this modelling approach is to determine the fertilisation success of different males under the assumption of postcopulatory female choice. The model mimics the essential features and possible functions of a reproductive tract with two (or more) separate sperm stores, which in principle enables the female to selectively store and use the ejaculates of different males. By comparing results of the mathematical model with experimental evidence, mainly from *Scatophaga stercoraria*, I address two questions: 1) Is there an advantage of having more than one spermatheca? 2) What are possible consequences of an uneven distribution of inseminations from different males between two (or more) separate spermathecae?

R. Hoess & A. Scholl (Zoologisches Institut, Universität Bern): The *Glomeris*-taxa *hexasticha* Brandt and *intermedia* Latzel (Diplopoda: Glomeridae): species or subspecies? – Allozyme data.

Diplopod species are usually distinguished by means of the gonopods of the males. *Glomeris* do not possess gonopods, and the telopods that males use to grasp the females' vulvae are similar in all species. Thus the color pattern of the tergites, often very variable, remains the only reliable feature for distinction. The taxa *hexasticha* and *intermedia* almost have the same color pattern and therefore are distinguished with reliability only by means of the form of the hind margin of the last tergite. Most myriapodologists presently consider *intermedia* as a

subspecies of *G. hexasticha* because of its vicariant distribution, even though in the beginning of this century Verhoeff raised it to species rank.

Based on a biochemical analysis using enzyme electrophoresis, we found very low genetic similarity between *hexasticha* and *intermedia*. Compared with three other clearly distinct *Glomeris* species, *G. intermedia* proved to be more closely related to *G. conspersa* and *G. transalpina* than to *G. hexasticha*. Both *G. hexasticha* and *G. marginata* are only distantly related to this trio. Consequently, *G. intermedia* must be treated as a bona-fide species.

R. Holderegger (Institute of Systematic Botany, University of Zürich, Switzerland): *Anemone nemorosa*: seed bank, germination and the effect of litter removal.

Anemone nemorosa L. is a dominant spring geophyte in the herb layer of different woodland communities in Central Europe. From the literature, seedlings are considered to be rare, germination rate to be low in (nature and in culture), recruitment to be irregular, and vegetative reproduction by clonal growth to be the main local dispersal agent. Litter removal experiments in a beech forest near Zürich, Switzerland, showed substantial germination of *A. nemorosa* in plots where litter has been removed as well as in control plots with litter. Litter removal strongly enhanced germination. A mean of 47.8 seedlings per square meter was found in plots where the litter was removed. A significant correlation between seedling number and ramet density within the plots implied dominant short-distance seed dispersal. Surprisingly, no diaspores of *A. nemorosa* could be detected in the seed bank. According to these results, sexual reproduction in the self-incompatible *A. nemorosa* may be as important as vegetative reproduction for the maintenance or increase of its local populations and in the determination of intrapopulational genetic structure. The genetic variation within populations of *A. nemorosa* will be investigated with isozymes electrophoresis.

C. Huber (Zoologische Aussenstation der Universität Zürich, Seestrasse 185, 8802 Kilchberg): Interspecific sperm competition in viviparous snails.

Until now, sperm competition was investigated exclusively within species. Especially when females mate with more than one male there is likely to be competition among the sperm for success at fertilizing the available eggs. This situation arises between species too, if two species hybridise in nature and females mate with males of both species. I investigated the possibility of interspecific sperm competition between the freshwater snail species *Viviparus ater* and *V. contectus*, which hybridise in Lake Garda, Italy. In previous crosses, virgin *V. ater* females mated to *V. contectus* males produced half as many offspring as intraspecific *V. ater* crosses, while the reverse combination was almost sterile. In my experiment I allowed 24 virgin *V. ater* females to mate once each with a *V. ater* and a *V. contectus* male, isolated the females and counted their offspring during 14 months. Hybrid offspring can be visually identified by the hair on their shells (*V. ater* offspring have none). Seventeen females produced 193 *V. ater* and 74 hybrid offspring. Three enzyme systems fixed for different alleles in the two species confirmed the visual identification of both *V. ater* and hybrids in 99% of all examined individuals. In the first two months, equal numbers of hybrid and *V. ater* offspring were produced. Then the number of both types of offspring declined, the decline being faster with hybrid than *V. ater* offspring. My interpretation of these results is that sperm competition did not occur, possibly because two matings did not provide enough sperm to ensure normal offspring production throughout the experimental period, and that *V. contectus* sperm can be equally successful in fertilising *V. ater* eggs as conspecific sperm.

M.J. Hutchings (School of Biological Sciences, University of Sussex, Falmer, Brighton, Sussex, BN1 9QG, UK): The role of heterogeneity in structuring clonal plant populations and plant communities.

The availability of essential resources is heterogeneous in space and time in most habitats. Despite this, measurements of the spatial and temporal scales at which resource provision is heterogeneous, and of levels of contrast of resource provision, are scarce. Information on the effects of habitat heterogeneity on the performance of plants has also been lacking until recently. Some of the information now available will be reviewed using studies of the clonal species *Glechoma hederacea*. It is now well known that *G. hederacea*, and many other plant species, are able to respond to heterogeneous resource distribution either through morphological or physiological plasticity, and that these responses can enhance resource acquisition and growth. Some of the effects of heterogeneous resource provision on performance will be illustrated, and predictions will be made about possible consequences for the composition of plant communities.

B. Imhoof & P. Schmid-Hempel (Experimentelle Ökologie, ETH Zürich): An endoparasite in a social insect: influence of the trypanosome *Crithidia bombi* on colony development of the bumble bee *Bombus terrestris* in the field.

Crithidia bombi is an endoparasite of bumblebees and is vertically transmitted within their colonies. Because it is horizontally transmitted between colonies and because it occurs in multiple infections inside one host it could afford to be very virulent, according to current standard theory. However, laboratory experiments comparing infected and uninfected bumblebee colonies revealed only mild effects, e.g. a delay in the production of males and young queens, but no reduction in number. In addition, *Crithidia bombi* did not affect the lifespan of bumblebee workers.

In the spring of 1995 I placed 16 colonies of *Bombus terrestris* infected in the lab and 16 uninfected colonies in three field sites. I monitored *Crithidia* infections in the faeces of the workers. All colonies became rapidly infected. Time to infection decreased over the season. There was no difference in the number of males and young queens produced in lab-infected or field-infected colonies, nor in the time span to their production after the placement in the field. The number of sexuals produced differed between locations. *Crithidia bombi* seems to be a parasite with very efficient transmission, but with very low virulence. In winter it is limited to vertical transmission by young queens. Therefore, the damage it can do to a colony is limited. It may even evolve towards mutualism to assure a sufficiently high production of young queens in infected nests.

P.M. Kareiva (Dept. of Zoology, University of Washington, 106 Kinkaid Hall, Seattle, WA 98195, U.S.A.): Detecting the consequences of global change: too many effects, too many causes and too few data.

As ecologists attack "big problems" such as landscape change or climate change, it is hard to know where to start. I will discuss a variety of approaches ranging from simulation models, to manipulative experiments, to long-term observations, to simplistic analytical theory. Each approach offers insights into the risks of habitat fragmentation and climate change, yet each also has severe limitations. I argue for using all approaches, and for being more ambitious in our efforts to address these pressing environmental problems using basic ecological theory. The organisms discussed will include Spotted Owls, pond-dwelling amphibians, endangered plants and animals in the United States, plant-insect-predator associations, and of course, "virtual organisms" in a computer.

L. Kohli, O. Daniel, F. Schönholzer & J. Zeyer (Soil Biology, Institute of Terrestrial Ecology, Swiss Federal Institute of Technology): Effect of the plant litter quality on the feeding rate of *Lumbricus terrestris*.

The effect of plant litter quality on a terrestrial food chain was investigated in a fallow (ecological compensation area) and in a plantation of the Japanese Pampas grass (*Miscanthus*

sinensis). Twelve different plant species were selected for the study and the food chain considered included plant litter --> bacteria/fungi --> *Lumbricus terrestris*. The content of polysaccharides (cellulose and non-cellulose) in the plant litter was quantified chemically and the growth of bacteria/fungi in the litter was followed by using specific staining techniques and automated image analysis. The feeding rates of *L. terrestris* were studied under field conditions and in microcosms.

Many plant species used in ecological compensation areas were suitable food resources for earthworms. The feeding rate depended on the plant species and was about 70% of the withdrawal rate. Field experiments with selected plants revealed a similar pattern of feeding and withdrawal. Feeding was positively correlated with bacteria in plants and negatively with cellulose content.

A. Krismann (Zoologisches Museum der Universität Zürich, Winterthurerstr. 190, 8057 Zürich): The suitability of moths to evaluate adjacent areas in different biotopes.

The use of moths by conservationists as bio-indicators is controversial because they are believed to fly long distances and so not to be habitat specific. I examined if the numbers of moth species and individuals differed between areas with different management regimes. I caught moths in 48 lighttraps in experimental enclosures and adjacent areas in a meadow and a pasture near the top of the "Schwäbische Alb" (southern Germany). The numbers of species and individuals differed significantly inside and outside the enclosures, especially for the Microlepidoptera. I also caught moths with light traps in a nearby forest, where the numbers of species and individuals was highest. The numbers were lowest in the meadow. Catches were also strongly positively correlated with maximum daytime temperature. This work suggests moths can be suitable bio-indicators to distinguish habitats. In a parallel study I compared arthropods caught in pitfalls and yellow bowls (Gelbschalen) in the same three habitats. They were equally useful in differentiating the habitats, in particular by identifying Hymenoptera.

S. B.M. Kraak & B. Mundwiler (Abteilung Verhaltensökologie, Universität Bern): Field data on the duration of egg collecting phase of the nesting cycle of the Three-spined Stickleback.

In 1953 van Iersel published a thorough causal study on the factors that induce the transition from courtship behaviour to parental behaviour in the male Three-spined Stickleback, *Gasterosteus aculeatus*. He found that at a certain moment in the nesting cycle, a male stickleback will stop courting additional females and collecting additional clutches of eggs, and will devote his time entirely to the care of the present brood until independence of the offspring. The relevant factors that were found to induce this transition are the number and the age of clutches in the male's nest. Recently, theoretical models have focused on the functional aspects of this transition. Since 1953, stickleback researchers have often cited van Iersel, when stating that male sticklebacks stop collecting eggs after 3 to 4 days. However, one must bear in mind that van Iersel's study was conducted in the laboratory under only a few, strictly controlled, conditions. We present for the first time data on the actual duration of egg collection by male sticklebacks in the field, under natural conditions. Not only did we find that the egg collection phase is often much longer than 3 to 4 days (up to 10 days), but also we found a large variation among males, and a decrease in the duration of the egg collection phase in the course of the breeding season. The variation in the duration of the egg collection phase will be discussed in the light of theoretical considerations.

C. Lang & O. Reymond (Conservatoire de la faune, Saint-Sulpice): Oligochaetes, organic sedimentation and trophic status: how to assess the biological recovery of sediments in lakes?

Oligochaete communities were used to assess the biological recovery of sediments after the abatement of eutrophication in Lake Geneva (Switzerland). In 1995, mean relative

abundance of oligotrophic worm species (OS) was around 30% in areas of low organic sedimentation (LOS) whereas, in areas of high organic sedimentation (HOS), it was below 15%. The abundance of OS observed in LOS areas was close to the value predicted from total phosphorus (TP) concentrations in the water. Accordingly recovery from eutrophication proceeded at the same place in the water (TP) and in the sediment (OS) of LOS areas, whereas it was delayed in the sediment of HOS areas. Lake Geneva was mesotrophic according to the oligochaete communities of LOS areas, but it was meso-eutrophic according to those of HOS areas.

C. Lavigne, X. Reboud & J. Gasquez (Institut für Umweltwissenschaften, Universität Zürich, Irchel), (Lab. de Malherbologie, INRA, BV 1540, 21034 Dijon cedex, France): Risk assessment of the release of herbicide resistant crops: importance of the cost associated with the resistance and its measurement in two crop species.

Applications for the commercial release of herbicide resistant crops, the majority of which transgenic, are becoming more and more frequent. The ecological concerns raised by their large scale use calls for risk assessment studies. By modelling the dispersal of such resistance genes with different genetic bases outside the field grown with the resistant crop, we show that the cost associated with the resistance (defined as the decrease in fitness of the resistant line compared to the susceptible one when no herbicide is applied) is the main parameter explaining the expected frequency of resistant plants outside the field.

Such a cost was tentatively measured in two crops, Foxtail Millet (*Setaria italica*) and White Chicory (*Cichorium intybus*) for which nearly isogenic susceptible and resistant lines were available. Resistance to atrazine was found to decrease the growth rate of the resistant line of Foxtail Millet whereas the sulfonyleurea resistant line of Chicory did not differ significantly from the susceptible one. This suggests that this latter resistance gene would not be selected against if it escaped to populations of wild Chicories. The ecological consequences of our results will be discussed in relation to the biology of the species.

E. Mitchell, A. Buttler, J. Gobat, J. van Leeuwen, P. van der Knaap, B. Ammann & B. Warner (Botany Institute, University of Neuchâtel, Switzerland; Geobotany Institute, University of Bern, Switzerland; University of Waterloo, Ontario, Canada): Forest clearance in the early 19th century, an indirect cause for the present abundance of pine (*Pinus uncinata* ssp. *rotundata*) in the Jura bogs?

The important pine cover of most bogs in the Jura mountains is sometimes believed to be the result of a natural succession and therefore interpreted as a climax vegetation. However, pollen records show that the present abundance of pine is relatively recent and therefore appears to be artificial. Some authors suggested that these trees have been planted in the bogs or that they spread as a result of drainage, but the question is still debated. A multidisciplinary study was undertaken in the Praz-Rodet bog in the Vallée de Joux (Swiss Jura) using testaceans (Protozoa: Rhizopoda), plant macrofossil and pollen analyses. The results suggest that there is a long history of pine presence in the bog, but that until the early 19th century it was much less abundant than today. Pine spread over the bog after the surrounding forest was cleared to create new pasture. It is suggested that before that time, the bog was protected from summer hydric stress by the surrounding forest. Forest clearance suddenly exposed the bog much more to wind, which increased summer evapotranspiration, lowered the water table, and finally allowed pine to spread over the bog. Implications of this theory on bog conservation in the Jura are discussed.

A. Monsutti & N. Perrin (Institut de Zoologie et d'Écologie animale, BB, Université de Lausanne): Life-history responses to size-dependent predation in *Physa acuta* (Gastropoda).

Life-history theory predicts that an organism's resource allocation patterns should depend on extrinsic mortality factors. Adaptive response to changes in mortality regime may arise through either genetic evolution or phenotypic plasticity.

To investigate these topics, we subjected experimental populations of the freshwater snail *Physa acuta* to different mortality patterns. One predator (*Macrostomum* sp.) feeds only on small juveniles (up to 2 mm). Theory in this case predicts a shift in prey life-history towards larger offspring. The other predator (*Dugesia polychroa*) feeds on adult snails as well, but only up to 6–7 mm. In this case, theory predicts shifts towards both larger offspring and larger adults. These precise shifts were observed in the experimental populations within 3 months of coexistence with predators.

Macrostomum presence induced a shift towards larger eggs, but did not affect *Physa* adult size. By contrast *Dugesia* induced shifts towards both larger adults and larger eggs. Since some of these responses to predation might be indirect, we performed analyses of partial effects as well as density-manipulation experiments. Predator presence remained the most significant factor responsible for the observed shifts. We conclude that *Physa acuta* can adjust on a plastic basis important life-history traits to the presence of different types of predators.

L. Passera, E. Roncin, B. Kaufmann & L. Keller (Universités de Lausanne et Berne): Increased soldier production in ant colonies exposed to intraspecific competition.

The most familiar examples of the advantages arising from division of labour and caste differentiation come from social insects. It has been suggested that the proportion of workers of various physical castes has evolved to enhance the fitness of colony members with the prediction that caste ratios should vary with environmental factors such as predation, competition and food availability. We experimentally tested this prediction in the ant *Pheidole pallidula* by comparing soldier production between colonies in which workers perceived the presence of foreign-colony workers and control colonies with no contact between foreign colonies. As predicted by caste ratio theory *P. pallidula* colonies increased soldier production in response to the presence of foreign workers. This is the first experimental evidence of a social insect altering physical caste ratios in relation to environmental factors.

J. Perritaz, A. Grub & H. Müller-Schärer (Institut de biologie végétale/écologie, Université de Fribourg; Eidg. Forschungsanstalt Liebefeld, Bern): Conservation of endemic wheed flora in Winter Wheat: comparison of weed- and wheat-development between acid and alkaline soils.

The studied strip management involves the conservation of a strip of 6 m to 12 m in width along the border of crop fields, where no herbicide and fertiliser treatments are applied. It constitutes a type of ecological compensation recommended in Integrated Production system in Swiss agriculture, aiming at the enhancement of species biodiversity by conserving the endemic flora of companion plants ("weeds") in crops. Fourteen fields of winter wheat of varying soil pH were selected in the canton of Fribourg (CH) and in each field, a control (common agricultural practice) and a strip treatment (with no herbicide and fertiliser) were applied in a plot of 6 m x 12 m. Number of plant species and number of individuals were greatly increased by 400% and 300%, respectively, in the strip plots as compared with the control plots, but weed biomass was only increased by 200% resulting in a 50% reduction of crop biomass. Number of plant species emerging from soil samples were positively correlated with the observed number of weed species in the strip plots. Here, the number of individuals, but not of species, was

significantly higher in acid soils ($\text{pH} < 6.0$) as compared with alkaline soils ($\text{pH} > 6.0$). Thus with regard to augmenting species biodiversity, both soils types are equally suitable, but weed pressure (biomass) is expected to be lower on alkaline soils.

I.R. Sanders, M. van der Heijden, R. Streitwolf-Engel, T. Boller & A. Wiemken (Botanisches Institut, Universität Basel): Arbuscular mycorrhizal fungi as driving forces of plant population and community structure.

Arbuscular mycorrhizal fungi (AMF) grow on the roots of 90% of vascular plants, with which they form mutualistic symbioses. Although AMF have already been shown to improve plant growth and to be strong determinants of floristic diversity, little attention has been given to understanding the ecological effects of different AMF species (or types). Studies comprising part of the Swiss Biodiversity Programme have focused on the effects of different species of native AMF on life histories, and reproductive strategies in plants and, consequently, as determinants in the structuring of plant communities. Our results from several studies combined suggest that: 1. Colonisation by different AMF isolates can alter the reproductive strategy of some plant species, in some cases affecting whether a plant is likely to reproduce clonally or sexually. 2. That plant species differ in how they will respond to different AMF isolates and that for some plants AMF diversity could be more important in determining the population structure than in other species. 3. That AMF diversity should be a strong determinant of plant community diversity in terms of the species composition and community structure and in the diversity of populations making up the community.

A. Sierro (Swiss Ornithological Institute, Sempach): Foraging activity and diet of *Caprimulgus europaeus* in Valais, South Switzerland: implication for conservation and landscape management.

Foraging by Nightjars away from their nesting areas has already been observed in the south of England. The birds preferred deciduous or mixed woodland habitats, while they avoided conifer plantations and arable or improved grassland.

In central Valais, similar observations have now been made in a pine wood in the immediate vicinity of vineyards. In 1994, 3 male Nightjars were fitted with glue-on radiotransmitters during Spring and early Summer. Each bird was followed from two fixed antennas during 5 to 13 nights; their locations were recorded every 5 minutes. In order to understand the significance of these regular flights away from the forest, three light traps were installed to catch flying insects at different locations from early June to mid August. The three main habitats, open woodland, hedgerows, and intensively cultivated vineyards were chosen. The discovery of a nest allowed the taking of 16 food samples brought by the adults to one nestling. The results showed a clear preference for open woodland (61.3% of locations) and steppes or hedgerowed cultures (31.4%). Nightjars clearly avoided intensively cultivated vineyards, even if some sightings were made over this habitat (5.6%). 1.7% of sightings were recorded in artificial environments. The home range of the unmated male was much larger than those of the two mated males. The farthest records of displacement were more than 2 km. The bulk of the diet consisted of Lepidoptera (83%), Neuroptera (14%), Diptera (2%). The most visited habitats were related to the richest food availability. However, the hedgerowed vineyards were less visited, while they are often richer than the woodlands. The trapping methods of insects are probably responsible for this bias. The nightly visits to the hedgerowed vineyards highlight the necessity of revitalisation of the most intensively cultivated areas and a global protection concept for Nightjar conservation.

N.C. Stenseth (Department of Biology, University of Oslo, P.O. Box 1050 Blindern, N0316 Oslo, Norway): Regional determinants of vole population cycles in Northern biomes.

The paper focuses on the population dynamic patterns of northern vertebrate populations as deduced from time series data on abundances. The deduced temporal patterns are

interpreted on the basis of general ecological models. A general discussion is first presented where it is argued that the population dynamics of vertebrate populations are either only regulated from above or both from above and below; they are never likely to be regulated only from below unless the region is too arid for a predator level to exist. This is argued to be unlikely for the boreal system. Three vertebrate systems in the boreal zone are discussed:

1. The small rodent population cycles in Fennoscandia: North of 60 degree, cycles are found in all studied microtine populations. As going north from 60 degree, the length of the cycle as well as the amplitude of the cycle increases. In statistical terms, this gradient is appropriately described by a clinal gradient in the first order autoregressive parameter (of a second order log-linear autoregressive model). The cyclic nature of the microtine rodents are argued due to specialist predators such as mustelids; the clinal structure in Fennoscandia is argued due to a gradient in the abundance of generalist predators. That is, a predator-prey model is assumed appropriate and the microtine rodents in Fennoscandia are argued to be regulated from above.

2. The grey-sided vole in the northernmost part of Hokkaido: Data from 90 populations are discussed (this being a subset of a much larger set); these populations are all found in the boreal zone. A gradient from the western coast to the mountains in the interior part of the island is found – along the coast only seasonal fluctuations are found whereas multiannual cycles (of the kind seen in Fennoscandia) is found. This population dynamic gradient is due to a clinal gradient in the second order autoregressive parameter; this is furthermore argued due to changing snow cover (with more and longer snow cover in the mountainous interior part of the northernmost part of Hokkaido). Again, a predator-prey model (and regulation from above) is argued to be appropriate; however, even though the geographic pattern in the population dynamic characteristics are superficially similar to those seen in Fennoscandia, the causes of the observed biogeographic patterns in Fennoscandia and in Hokkaido are argued due to different processes (generalist predators and snow cover, respectively).

3. The snowshoe hare and lynx dynamics (as seen in the Canadian boreal zone): It is shown that the dynamics of the snowshoe hare is appropriately seen as a three dimensional process (where the hare dynamics is controlled both from below and above), whereas the lynx is appropriately seen as a two dimensional process (where the lynx dynamics is controlled only from below – the top predators presumably being too scarce to be of any major influence). Ecological models developed on the basis of the statistical analyses are found consistent with available data (including experimental data).

The paper is concluded by a discussion of the importance of environmental stochasticity in northern ecosystems (such as the boreal forests). This is done in the framework of a discussion of the relative importance of non-linearity and environmental stochasticity: If the process is strongly non-linear, environmental stochasticity is not necessary in order to sustain the population cycles seen in northern ecosystems. However, if the process is not strongly non-linear, then the deterministic part of the system (primarily determined by biotic interactions within the system) may be seen to determine the periodicity of the periodic fluctuations whereas the environmental stochasticity (e.g., perturbations due to factors such as weather) may be seen as the factor sustaining the cyclic nature of the population dynamics.

As a side issue, the issue of chaos is in this connection touched upon: it is suggested that – consistent with the results of testing for non-linearity – there is no clear indication of chaos in the northern vertebrate populations discussed above. This is partly shown by calculating confidence intervals for point estimates of the dominant Lyapunov exponents for the analysed time series. The same conclusion is also reached by another avenue studying the cyclic process as such.

As a post script, some reflections are advanced in the form a general discussion of the need for combining the study of patterns (as deduced from long term time series data) with the study of processes (as, e.g., deduced from experimental studies). Indeed, it is argued that experimental and theoretical ecology must be combined with natural history type of approaches. It is finally argued that this merging most efficiently is done by combining statistical modelling and mathematical modelling. Examples of this is given throughout the paper.

H.B. Stutz (Zoologisches Museum, Universität Zürich): Population estimates of *Myotis myotis* in Switzerland.

Over a period of six years (1990–1995) the maximal number of adult individuals (mainly females) was estimated for 60 maternity roosts of *Myotis myotis*/*blythii* in the eastern parts of Switzerland. From May to mid-July, bats were counted at daytime while roosting or at dusk when emerging from their roosts. To estimate the whole population of *Myotis myotis*, the following unknown factors, besides the comparability of counting methods, have to be taken into account: the number of individuals of the sibling species *Myotis blythii* in approximately 10% of the maternity roosts, adult males outside the maternity roosts, unknown maternity roosts, exchange of individuals with colonies outside the study area. Estimating these factors by means of hypotheses derived from literature and taking into account the mean values of the years '93, '94, '95, a total number of approximately 21'500 adult individuals of *Myotis myotis* can be calculated. In comparison to similar population estimates of *Myotis myotis* in some parts of Germany, the Swiss population density is only half this size. But altitude distribution of *Myotis myotis* in relation to the specific topographic situation in the eastern parts of Switzerland could highly influence our estimate.

M. Tschan, A. Aebischer & D.R. Meyer (Institute of Zoology, University of Fribourg): Is food availability related to territory quality or breeding success in the Savi's Warbler?

The Savi's warbler (*Locustella luscinioides*; Sylviidae) winters in West Africa. The breeding site under investigation is 17 ha and consists of continuous, inundated reed and sedge stands; it is situated at the Southern shore of Lake Neuchâtel. A discriminant analysis based on eleven parameters of vegetation structure was performed in order to find the canonical function that provides the best segregation between territories, and pseudo-territories randomly generated on paper. The score on the axis of the discriminant function correlated negatively with the male/female arrival date and positively with male/female breeding success. (Aebischer *et al.* 1996). The food availability in the territories (insect larvae and freshly metamorphosed adults of water insects) was measured by collecting all invertebrates on small plots. It does not correlate with territory score nor with the arrival dates of males.

We erected observer platforms to survey the foraging excursions of selected birds feeding young. We noted that 78% of all excursions (always on the ground) lead outside their proper territory, into nonoccupied land. Video monitoring of nests and analysing neck ring probes revealed that for the first brood 55% of the fed biomass consists of freshly hatched dragonflies, later in the season the warblers become more generalist in behaviour. The biomass fed per hour per young decreases slightly with the season, the feeding frequency increases.

T. Turlings (Institute of Plant Sciences, Applied Entomology, ETH Zürich): Do herbivore-damaged plants protect themselves by attracting parasitic wasps?

Plants that are under attack by herbivores initiate the release of highly specific volatiles. The emissions of these plant volatiles result in an odor that is used by natural enemies of the herbivores to locate the damaged plants. Recent studies have shown that parasitic wasps make effective use of these odors. It is tempting to suggest that the plants emit the odors to lure in the parasitoids and predators for their protection. If indeed the plants emit an odorous signal to broadcast the presence of herbivorous insects to natural enemies of the herbivores, such a signal would be particularly effective if: 1) The signal is easily detected by parasitoids and clearly distinguishable from background odors. 2) The signal is specific enough that it would enable the parasitoids to recognize plant damage that is done by suitable hosts. 3) The emission of the signal occurs shortly after the herbivore starts feeding and is emitted at the time that the natural enemies forage. Evidence that support or contradict these three criteria for an useful signal will be presented. The controversy concerning the function of herbivore-induced emissions of plant volatiles will be further discussed.

C. Wedekind & M. Milinski (Abt. Verhaltensökologie, Zoologisches Institut, Universität Bern, 3032 Hinterkappelen): Do sticklebacks avoid consuming copepods, the first intermediate host of *Schistocephalus solidus*? – An experimental analysis of behavioural resistance.

Many parasites that use intermediate hosts are transmitted to the next host through predation. If the next host's fitness is strongly reduced by the parasite, it is under selection either to recognize and avoid infected intermediate hosts or to exclude that prey species from its diet when alternative prey are available. We investigated the predator–prey interaction between laboratory bred Three-spined Sticklebacks (*Gasterosteus aculeatus*), the second intermediate host of the cestode *Schistocephalus solidus*, from two parasitised and one unparasitised population, and different prey types: infected and uninfected copepods and size-matched *Daphnia* as alternative prey. Copepods with infective proceroids were more active, had a lower swimming ability and were easier to catch than uninfected controls. The sticklebacks preferred moving copepods. Therefore parasitised copepods were preferentially attacked and consumed. There was no effect of the sticklebacks' parent population being parasitised or not. The sticklebacks switched from *Daphnia* to (uninfected) copepods in the course of a hunting sequence; this switch occurred earlier in smaller fish. With this strategy the fish maximised their feeding rate: *Daphnia* were easier to catch than copepods but increasingly difficult to swallow when the stomach was filling up especially for smaller fish. However, there was no indication that sticklebacks from infected populations either consumed *Daphnia* rather than copepods or switched later in the hunting sequence or at a smaller size to consuming copepods than fish from an uninfected population. Thus, sticklebacks did not avoid parasitised prey although *S. solidus* usually has a high prevalence and causes a strong fitness reduction in its stickleback host.

M. Weggler (Zoologisches Institut, Universität Zürich): Why do some males look like females in passerine birds?

Male passerine birds of several species adopt for their first breeding season a dull-coloured, female-like plumage. Delayed plumage maturation is viewed as an adaptation to enhance breeding success and/or survival of sexually mature but still inexperienced males. Female-coloration in males could either function as a dishonest signal (female mimicry) to gain access to breeding opportunities or copulations deceptively. Alternatively it could work as an honest signal to avoid aggression in territorial combats (aggression avoidance) or it could simply be a moult constraint without measurable fitness consequences. I tested these hypotheses using the Black Redstart *Phoenicurus ochruros* as my study organism. A bimodal morph distribution in first year males with males either indistinguishable by sight from females or males that look like adult males provides the unique possibility to separate effects of age from effects of coloration in this species. Preliminary results analysing primary and secondary reproductive success of an alpine population studied for two consecutive years do not favour the female mimicry hypothesis.

A. Widmer & P. Schmid-Hempel, A. Estoup & A. Scholl (ETH Zürich, Institut für experimentelle Ökologie; Laboratoire de Génétique des Poissons, INRA, France; Zoologisches Institut, Universität Bern): Genetic differentiation and gene flow in the pollinators *Bombus pasquorum* and *B. terrestris* (Hymenoptera).

Levels of genetic differentiation among populations are the result of both historical and present day processes. Historically, cycles of glacial and interglacial periods have repeatedly disrupted formerly continuous distributions. Populations survived cold periods in isolated refugia from where recolonisation occurred. These processes have had major impact on the amount and distribution of genetic variation within and among populations. Whether these historical traces are still evident in present-day populations mainly depends on the level of gene flow and drift. We studied the genetic population structure of two pollinators, the bumblebees

Bombus pascuorum and *Bombus terrestris*, using microsatellite markers. We found that the levels of genetic differentiation among European populations strongly differ in the two species. We discuss these results with respect to historical and present-day scenarios.

A. Wust-Saucy (IZEA, University of Lausanne, 1015 Lausanne): Phylogeography and genetic differentiation of the ecological forms of the water vole, *Arvicola terrestris*, in Europe.

Arvicola terrestris is a highly polymorphic species with a wide geographic distribution covering most Eurasia. The many (more than 35) subspecies described by taxonomists can be grouped according to their ecology into semi-aquatic and fossorial forms. The significance of these two forms, which are differentiated by characters such as body size, colour, weight, population dynamics, home range size, mating behaviour and habitat, is still controversial. The sequencing of the cytochrome b gene of the mitochondrial DNA shows a genetic divergence between the two ecological forms of *Arvicola terrestris*. Furthermore the phylogenetic analyses describe the fossorial populations as monophyletic whereas the aquatic ones as polyphyletic. Eventually the study of the European phylogeography of this species allows us to propose some historical hypotheses to explain its present distribution.